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THE ECOLOGIC SUBTERRANEAN ANATOMY OF SOME PLANTS OF A PRAIRIE PROVINCE IN CENTRAL IOWA

ADA HAYDEN

INTRODUCTION

A survey of the literature pertaining to functional and adaptational features of subterranean organs as related to their morphology shows this subject to have been less investigated than that of leaf structure. Though there has been considerable work done in the field of pure morphology, that too is yet deficient in many respects. Descriptions found in Gray's Manual of Botany (8) and Britton and Brown's Flora (1) have either no reference to subterranean parts or only incomplete ones.

The subterranean organs of prairie plants are of two classes, roots and subterranean stems. Of course all these plants have secondary, *i. e.*, absorbent or collecting roots, but in many plants the subterranean stems are intermediate structures connecting collecting roots with conducting aërial stems and therefore assume the function of primary or main roots.

Prominent subterranean stems are seen in the majority of alluvial basin plants and in modified abbreviated form in the upland plants, especially in the grasses and composites which constitute the majority of the upland plants.

It was the object of this study of subterranean stem and root types (*a*) to note whether variations were correlated with habitat; (*b*) to determine whether the stems were equivalent to or advantageous to the root in the economy of the plant.

The *functions* of subterranean organs are *storage*, *anchorage*, *absorption*, *conduction*, and *propagation*. Anchorage in the case of prairie plants may be dismissed, for most of them are low, have a compact habit of growth, and are not particularly subject to uprooting. As to *propagation*, the fact that subterranean stems have numerous nodal buds while roots have adventitious buds, if any, gives subterranean stems, especially rhizomes, the advantage as propagators. Concerning *storage*, the root and the subterranean stem seem to be equally well equipped, though this question will be discussed under anatomical structure.

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Methods

The material was stored in 50% alcohol, and after free-hand cutting the sections were stained with a solution of water-soluble safranin, followed by haematoxylin, cleared in cedar oil and clove oil, and mounted in Canada balsam. The drawings of the subterranean structures were not made to a single scale because the large size of some of them made this impracticable, and also because of the variability in size, which makes the comparison of the size of the roots and stems of species less important than the relative proportion occupied by the tissues of the roots compared.

Historical

Some progress has recently been made in classifying subterranean organs; among the valuable contributions are those of Cannon (2), Harshberger (11), Holm (13), Yapp (18), Dauphiné (6), Constantin, Jodin (15), and Maxwell (16).

Maxwell (16) reviews the history of the histological study of roots, which before 1865 were studied as masses of tissues and after this period with reference more directly to the origin of organs.

According to Cannon (2), the work of Rimbach, Büsgin, and Friedenfeldt as reviewed by Von Alter (Wurzelstudien, Bot. Zeit. **67**: 175. 1909) is important because their researches indicate that the root systems of flowering plants may be divided into two groups according to the character of the terminal roots; they are either *intensive* or *extensive*. Intensive root systems have fine terminal roots; they are richly branched and occupy small soil volume. Extensive root systems have coarse ultimate roots, are not richly branched, and occupy a relatively large soil volume. Cannon describes three main types of root systems found in the desert plants of the southwestern United States: (*a*) Root systems which extend horizontally from the main axis and lie for their whole course near the surface of the ground. (*b*) Root systems which are characterized by a strongly developed tap root going down directly to a depth determined in part by the character of the soil, in part by the penetration of the rains, and in part by the character of the root itself. (*c*) Roots that not only reach widely but penetrate fairly deeply. When the root is of an obligate type the distribution of the species is much restricted, but when it undergoes modification with changed environment the distribution of the species is much less confined.

Yapp (18) and Scherff (17), in their marsh studies, note the stratification of subterranean systems as well as the aërial portions of different species.

Holm (13) reviews a paper of Häckel (10) on the peculiarities of the grasses of dry climates, among which he distinguishes (*a*) *tuberous* and *bulbous grasses* and (*b*) *tunic grasses*. The tuberous and bulbous forms occur only in countries with periodic dry seasons. None have been observed in

the moist parts of the tropical region. The author does not regard these bulbs or tubers as reservoirs of starch or sugar, as is true of the similar organs of the Liliaceae and Iridaceae. Though they are structurally homologous with these, physiologically they are reservoirs. The author has shown that *Poa bulbosa* on being cultivated in moist soil almost loses its bulbous character. The second group includes forms in which the bases of the culms and shoots are covered with at least three faded sheaths. These all inhabit dry localities. In those forms which prefer damp or shaded places there is usually one faded sheath present, and even that disappears soon. *Straw tunics* are distinguished from *fiber tunics*; in the former the sheath remains complete although faded, in the latter the sheath breaks up into fibers. The function of these tunics is regarded as that of water conservation. Holm has contributed various studies on the morphology of subterranean portions of plants.

Gross Anatomy

In the alluvial basin region the prairie plants under observation show a prominent development of thickened, elongated rootstocks. The majority of these plants are Gramineae, Cyperaceae, and Compositae, in which this feature is a systematic character. The Cyperaceae are seldom found on the highland, but the upland members of the Compositae and Gramineae, while they retain their rootstock characters, have abbreviated forms. The Gramineae especially show abbreviated subterranean parts in the form of hard bulbous or corm-like thickenings from which the roots radiate, or of short hard rootstocks. *Panicum virgatum*, which has a wide range of habitat, growing either on upland or lowland, has hard, radially branching, slender, scaly rootstocks which are shorter in the drier upland habitats. *Spartina Michauxii*, which grows on lowland or in moist upland ravines subject to drought, shows shorter rhizomes on the upland. The Solidagos which frequent the ridges have very abbreviated, hard, corm-like subterranean stems, while those which frequent moist habitats have longer rhizome-like structures. The genus Liatris has a species with short, sheathed corm which grows on the hilltops and a species with an elongated, fibrous-sheathed tuber on the moister slopes. *Helianthus grosseserratus* has a short, thick rootstock, while *H. tuberosus* has a long, slender-stemmed tuber. *Silphium laciniatum* is provided with a deep root. The Compositae are variable, having short tubers, elongated rhizomes, corm-like structures, or tap and fascicled roots, which enable them to thrive in a wide range of habitats and probably account for their great numbers and diversity of forms. Among the Leguminosae are *Desmodium illinoense*, *Amorpha canescens*, *Lespedeza canadensis*, *Petalostemum purpureum*, and *P. albidum*, which are upland plants with deep, tough roots, usually having long, thick tap roots and somewhat smaller lateral roots. These leguminous plants and others with

similar root habits show little storage area but have prominent tracheae, which would indicate that they derive their moisture from a lower water table than do their short-rooted neighbors. Liatris shows few tracheae but much storage tissue. Ceanothus has also a deep, branched tap root. The exterior of the cortex of the roots is corky, leathery, fibrous-sheathed, or flaky-deciduous, while the subterranean stems have hard, scaly fibrous or straw sheaths which probably have the ability to hold water by capillarity as well as to prevent evaporation from the inner parts. These scaly coverings of thickened subterranean organs, especially of rhizomes, are prominent in both uplands and alluvial basins. Since conditions of drought are likely to occur frequently and especially in protracted periods during the latter part of the summer, these features are undoubtedly useful as a protection against desiccation. The swamp plants must be able to tolerate not only moisture to the point of saturation but drought as well. The roots of the upland plants may be regarded as of the intensive type, those of the lowlands as of the extensive type.

Minute Anatomy

The anatomical descriptions of the stems and roots studied have been made under the heads (*a*) Primary cortex, and (*b*) Stele, which portions of the stem and root are homologous. These structures show certain prevalent types which may be distinguished in the angiosperms as follows:

Monocotyledons—

Stem: concentric or collateral, endarch bundles.

Root: radial, exarch bundles.

Dicotyledons—

Stem: concentric, endarch bundles.

Root: radial, exarch bundles.

There is great diversity of structure shown by the representatives of different families and individuals thereof, whose morphological and physiological variations are discussed by De Bary, Solereder, Haberlandt, Stevens, Coulter, Barnes, Cowles, and others. Exceptions seem more abundant than cases of conformity to rules at the present status of correlation. Transformations from the original types take place with the secondary thickening process, in numerous instances to such an extent that the original type structures are hardly recognizable. Systematic relations have not been conclusively worked out, yet every species has in some degree established its economy of water relations, the indicators of which, in so far as experiment has proceeded, are shown to be primarily (*a*) *parenchyma* (storage and aerenchyma), (*b*) *mechanical tissue*, and (*c*) *conductive tissue*. The prominence of the latter two seems to indicate xerophytism and that of the first the reverse condition. *The relative proportion of these tissues in each individual stem or root has been used as a means of indicating its degree of xerophytism* in this study.

Before applying these tests perhaps the reasons for selecting them should be given. An examination of young water-absorbing roots shows them to have a *deep cortex bearing root hairs and a small vascular cylinder with distinctly radial bundles.* "In roots, any departures from the typical radial structure of the vascular strands are generally correlated with special environmental conditions, or arise from the necessity of increasing the amount of available conducting tissue" (Haberlandt). In a radial root there is no means of tangential increase, so this increase must take place in a radial direction toward the cortex and results in orienting a cambium which produces concentric layers of phloem and xylem. This is seen to be an advantageous structure in older roots whose function is conduction and not absorption from the cortical layer, for here there is no incoming stream of water to cross the proteid-conducting zone but only a rising central column. It is seen that such an arrangement is also desirable for resistance to strains which in roots are in a longitudinal direction. This solid cylinder gradually develops pith and assumes an annular vascular structure in the stem, from which bundles shoot out into the branches. Hence a root changes from a water-collecting to a water-radiating organ and the pith of the stem serves as a good collecting reservoir; though pith is sometimes absent. The stem, being subject to radial strains, is thus well adapted by its hollow-cylinder mechanical system.

Rhizomes (Haberlandt) *which fix the plant in the soil* agree with roots in having their mechanical tissues united to form a stout axile tube or a solid central strand; this centralization of the mechanical system is very marked in the rhizomes of grasses, sedges, and rushes, which, accordingly, when regarded from an anatomic-physiological standpoint, approximate more closely to roots than to the aerial stems of which they are the morphological equivalents.

Structural features (Solereder) *which vary with the amount of water in the soil* and air and with the degree of transpiration on the part of the plant, affecting chiefly the number of vessels and width of lumina, are of minor systematic value.

Kohl observed that certain plants (*Mentha aquatica*, *Thalictrum galeoides*, and *Menyanthes trifoliata*) develop more collenchyma and bast if grown in dry air, *i. e.*, under conditions favorable to transpiration, than they would if produced in a moist atmosphere, *i. e.*, with their transpiration reduced. Here it is impossible to state with certainty whether the process is adaptive or self-regulatory. It should, however, be noted that in the case of herbaceous plants growing in a dry atmosphere, or in fact under xerophytic conditions in general, turgor has a smaller mechanical value than usual because the risk of temporary wetting is so great in these circumstances that any decrease in the development of mechanical tissue must be advantageous. In general, there is correlation between the number of water-conducting vessels and the extent of the foliar transpiring surface.

Jost, by removing the leaves of seedlings of *Phaseolus multiflorus*, *Helianthus annuus*, and *Vicia Faba*, found that the vascular bundles supplying the amputated leaves remained rudimentary. There is evidence of a process of adaptive self-regulation.

Kohl has demonstrated that the water-conducting system may be reduced by growing the plants in a moist atmosphere, and Schenck has demonstrated the reduction of vascular bundles of *Cardamine pratensis* by growing the terrestrial plant in water. Plants which are naturally amphibious exhibit a similar character.

The endodermal layer has been a subject of considerable experiment and study. In some plants the cells of this layer have thickened inner walls, and in some the walls are of uniform thickness. Schwendener has shown that the endodermis is impermeable except in spots where it acts as side sluices in a system of irrigating canals, the main channels of which are represented by the vessels. Greatly thickened endodermal layers are found in marsh plants which live in places likely to dry up periodically. This is true of some plants growing in dry regions.

Gaseous exchange is slow under aquatic conditions and is accelerated by the presence of air spaces. Aerenchyma is also found in marsh plants subject to submerging.

These facts show that the relative distribution and proportion of mechanical tissue, parenchyma, and conductive cells are of considerable significance with reference to adaptation in the economy of plant tissues.

Description of Subterranean Organs

Typhaceae

Typha latifolia L.

Habitat: Alluvial basin; marsh.

Gross structure: Long, stout, horizontal rootstocks; 6–8 in. deep; soft and spongy, origin from a thick stem base; long, slender; straight roots, at notes, perennial (Plate XV, fig. *d*).

Histology of rhizome (Plate XVI, fig. 1):

Primary cortex: Radius of cortical area ½ radius of rhizome; hypodermis, thin-walled parenchyma; next a zone of rounded-compact parenchyma in which vascular bundles are originating; zone of aerenchyma in which vascular bundles have enlarged; bundles surrounded by woody sheath. Endodermis pronounced, with thick inner wall.

Stele: Composed of one row of large, woody bundles surrounding the pith cylinder of thin-walled aerenchyma, among which are scattered smaller vascular bundles with compact, thick, woody sheath.

Summary: Air space prominent; parenchyma well developed; vascular tissue fairly abundant; slight mechanical tissue, found only at sheath for bundles; vascular strands act as mechanical tissue in cortex.

Histology of root (Plate XVI, fig. 2):

Primary cortex: Composed of 4-sided to oval parenchyma cells; air space small; no mechanical tissue.

Stele: Radius 4/5 that of the root; conducting vessels fairly prominent, surrounded by parenchyma.

Gramineae

Phragmites communis Trin.

Habitat: Alluvial basin; edge of water, wet soil.

Gross structure: Long, creeping rhizome, thick, soft and spongy; scales at nodes prominent; clusters of roots emerging from nodes bearing fine secondary hair-like roots; rhizomes branch in several directions and at several levels; perennial (Plate XV, fig. *b*).

Histology of rhizome (Plate XVII, fig. 1):

Primary cortex: Radius equal to 1/2 radius of rhizome; epidermal cells small, thick-walled; hypodermis of thin collenchyma; parenchyma large-celled, hexangular, forming arches around large oval air cavities in a ring within cortical cylinder.

Stele: Hypodermis, 3 rows of collenchyma; main portion of vascular cylinder composed of large thin-walled parenchyma surrounding rows of alternately arranged vascular bundles; vascular bundles sheathed by wood fibers; one row of small bundles where arches of cortical parenchyma join vascular cylinder.

Summary: Rhizome characterized by prominent thin-walled cortical cylinder; mechanical tissue reduced; vascular bundles few.

Histology of root (Plate XVII, fig. 2):

Primary cortex; Radius 5/7 of root radius; hypodermis, 3 rows thin collenchyma; parenchyma of large oblong cells with long axes radially placed; large elliptical air spaces; endodermis prominent, with thick outer wall.

Stele: Composed of small thin-walled parenchyma cells with a ring of young radial vascular bundles in which the exarch arrangement of metaxylem and protoxylem is very distinct.

Summary: Young root composed almost entirely of thin-walled, loosely arranged parenchyma with prominent air space, only a trace of mechanical tissue.

Spartina Michauxiana Hitchc.

Habitat: Alluvial basin; wet ground; sometimes fairly dry locations.

Gross structure: Creeping radial rhizome; long, tough, hard; scaly; springs from a short, condensed base; perennial (Plate XV, fig. *h*):

Histology of rhizome (Plate XVIII, fig. 1):

Primary cortex: Radial depth 3/7 radius of rhizome; epidermis small-celled, thick, walled; hypodermis, 7 rows of collenchyma in which occasional small vascular bundles are embedded; clusters of compact, round parenchyma cells alternating with large air spaces constitute the inner arc of the cortex; endodermis thick-walled.

Stele: Sclerenchyma of 6 rows borders outer margin and hollow center of this cylinder; vascular bundles numerous, large, with prominent sheath of wood fibers; pith parenchyma relatively thick-walled; only a few cells of pith between bundles.

Summary: Parenchyma and air space reduced; mechanical tissue prominent; vascular bundles numerous, large.

Panicum virgatum L.

Habitat: Alluvial basin; low, wet soil; sometimes moist; dry upland.

Gross structure: Plant tufted, with long, creeping rhizomes; scaly, hard and tough perennial.

Histology of rhizome (Plate XVIII, fig. 2):

Primary cortex: Radius 2/9 that of rhizome; epidermal cells 4-sided, thick-walled, small; hypodermis, 7–8 rows of thick collenchyma; inner half of cortex composed of clusters of thin-walled, compact parenchyma alternating with large air spaces.

Stele: Vascular bundles large, numerous, surrounded by thick sheaths of sclerenchyma; pith parenchyma of 2–3 rows separating the bundles; bands of scleren-

chyma 3–4 cells deep bound the perimeter of the vascular cylinder and surround the hollow center.

Summary: Parenchyma poorly developed; air space small; mechanical tissue prominent; vascular bundles large, strongly sheathed.

Cyperaceae

Scirpus fluviatilis (Torr.) Gray.

Habitat: Alluvial basin; swamps.

Gross structure: Rhizome elongated, terminating in tuber-like swellings; radial growth; moderately thick; hard tuberous tip but spongy root-stalk; horizontal, descending; perennial (Plate XV, fig. *c*).

Histology of rhizome (Plate XIX, fig. 3):

Primary cortex: Radius 1/2 that of the rhizome; thin-walled, angled to oval parenchyma cells form a band 1/5 the depth of the cortex and send down rays to the vascular cylinder, forming arches around the large air spaces; endodermis cells distinct, of uniform thickness.

Stele: Just inside the endodermis one row of concentric vascular bundles strongly sheathed with wood fibers; woody sheathed bundles scattered through the parenchyma; parenchyma compact; thin-walled.

Summary: Air cavities prominent in cortex; parenchyma thin-walled; vascular bundles numerous; parenchyma fairly prominent in central cylinder.

Scirpus validus Vahl.

Habitat: Alluvial basin; margin of pond.

Gross structure: Rhizome stout, scaly; horizontal; linear extension; cortex soft and absorbent; vascular cylinder hard and flinty; fringes of slender roots with secondary hair-like branches radiate from the short nodes, appearing continuous not clustered; perennial (Plate XV, fig. *g*).

Histology of rhizome:

Primary cortex: Radius 1/3 that of the rhizome; air space prominent; parenchyma cells round, with 5–6 spoke-like, short cellular flanges forming a characteristic network; endodermis prominent with thick inner walls.

Stele: Solid; pith parenchyma cells round to oval, rather thick-walled; concentric bundles numerous around the outer perimeter of cylinder, but larger and fewer toward center; bundles thickly sheathed by centripetal arc of bast.

Summary: Aerenchyma prominent; this type of cell structure not only provides ample air space but insures mechanical strength; vascular tissue prominent.

Iridaceae

Iris versicolor L.

Habitat: Alluvial basin; margin of pond, swamp.

Gross structure: Rhizome thick, relatively short; tuberous swellings; horizontal; linear extension; roots slender, vertically descending, clustered at nodes; fine secondary branches; perennial (Plate XV, fig. *e*).

Histology of rhizome (Plate XIX, fig. 1):

Primary cortex: Radius 1/4 that of rhizome; 3 rows hypodermal mechanical tissue; a similar band of angular cells with slightly thickened walls bordering the inner arc of cortex; aerenchyma a hexangular network; endodermis thick-walled on inner surface.

Stele: Pith parenchyma thin-walled, compact, forming a small cylinder in center not entered by bundles; vascular bundles concentric, numerous around perimeter of cylinder, farther apart but larger toward center; woody sheath prominent.

Summary: Cortex with prominent aerenchyma; vascular bundles strongly reinforced.

Histology of root (Plate XIX, fig. 2):

Primary cortex: Radius 5/6 radius of root; hypodermis, 2–3 rows of collenchyma;

parenchyma thin-walled, compact, with oval areas filled with very large parenchyma cells, 6–8 times the size of the round parenchyma (these areas show signs of breaking up and will probably give rise to air cavities); endodermis with thickened inner wall.

Stele: Parenchyma of small angular cells; bundles radial; a ring of large protoxylem cells lying within radial strands of metaxylem.

Summary: Mechanical tissue undeveloped; parenchyma prominent; tracheal vessels large.

Polygonaceae

Polygonum Muhlenbergii (Meisn.) Wats.

Habitat: Alluvial basin; muddy or dry places, rarely in shallow water.

Gross structure: Root thick, descending, tough, smooth; rootstocks branching; scaly, branching from root at different levels; horizontal, radial extension; perennial (Plate XV, fig. *a*).

Histology of rhizome (Plate XX, fig. 1):

Primary cortex: Depth 1/6 radius of rhizome, epidermis thin-walled; rectangular cells; hypodermis, several rows of cork; aerenchyma occupies 9/10 of cortical space.

Stele: 1/6 radius of rhizome; bundles collateral; bast forming a slender zone bordering phloem; phloem cells large, 6-sided; xylem with large tracheae; wood parenchyma 4- to 6-sided, compact, thick-walled.

Pith: Depth 2/3 radius of rhizome; homogeneous aerenchyma.

Summary: Vascular cylinder forming a narrow, compact zone; remainder of stem composed of aerenchyma.

Histology of root (Plate XX, fig. 2):

Primary cortex: Depth 1/4 radius of rhizome; hypodermal cork fills 1/5 of cortical area; large-celled, thin-walled parenchyma fills 4/5 cortical area; endodermis not distinct.

Stele: Collateral bundles; cone-shaped rays of old phloem surrounded by clusters of sclerenchyma extend into the cortical parenchyma, young phloem of rectangular cells adjacent to cambium; xylem forms a solid, pithless cylinder of large open tracheae and small, thick-walled, 4- to 6-sided wood parenchyma; the exarch character of bundle is shown in the small primary cylinder.

Summary: Parenchyma of cortex thin-walled with thick protective layer of cork; little mechanical tissue in cortex; relatively thick, compact wood parenchyma cells form a solid cylinder.

Ranunculaceae

Ranunculus delphinifolius Torr.

Habitat: Ponds, rooting in mud; stems and leaves floating.

Gross structure: Slender, fascicled roots; succulent; perennial.

Histology of root (Plate XX, fig. 3):

Primary cortex: Depth 4/5 radius of root; epidermal walls slightly thicker than walls of parenchyma; parenchyma cells large, oval to round, thin-walled, spongy; air cavities at intervals, endodermis walls of uniform thickness.

Stele: Vascular bundles radial; protoxylem and metaxylem distinct; tracheal tubes small.

Summary: Parenchyma prominent, thin-walled; vascular tissue poorly developed; mechanical tissue absent.

Saxifragaceae

Heuchera americana L.

Habitat: Moist to dry slopes; upland.

Gross structure: Thick, irregularly branched, tough rhizome with small secondary roots; perennial.

Histology of rhizome (Plate XXI):

Primary cortex: Depth 1/5 radius of root; hypodermis of thin-walled cork cells occupying 1/6 cortex; thick-walled parenchyma forms a band around phloem; endodermis not distinct.

Stele: Collateral bundles; phloem cells 4- to 6-sided; 3–4 strands of xylem extend from the center of the root radially outward, alternating with broad radii of thin-walled oval to square parenchyma cells.

Summary: Parenchyma prominent; mechanical tissue undeveloped; tracheal tissue proportionally small; cork well developed.

Rosaceae

Potentilla arguta Pursh.

Habitat: Dry, rocky, gravelly or alluvial soil.

Gross structure: Root tap, fibrous; thick, hard, tough; perennial.

Histology of root (Plate XXII, fig. 1):

Primary cortex: Depth 1/6 radius of root; cork hypodermis, thick-walled, occupies 1/2 of cortex; thick-walled, large-celled, angular parenchyma.

Stele: Radial bundles separated by broad rows of oval-celled parenchyma pith rays which radiate from the center of the root, forming fan-shaped terminal expansions the edges of which extend around the phloem; phloem thin-walled; 4- to 6-sided; xylem in several annular rings; wood parenchyma thick-walled; wood fibers are scattered among the wood parenchyma and form solid rings at termination of yearly growth; tracheae large.

Summary: Protective cork well developed; tracheae large and numerous; mechanical tissue in form of wood fibers prominent.

Leguminosae

Petalostemum candidum Michx.

Habitat: Dry prairie slopes; near base of hill commonly, while *P. purpureum* occupies ridges.

Gross structure: Root thick, tough; deep tap with prominent secondary roots; tubercled; perennial.

Histology of root (Plate XXII, fig. 2):

Primary cortex: Depth 1/6 radius of root; cork hypoderm occupies 1/4 of cortex; parenchyma large, angular, fairly thick-walled cells; endodermis not distinct.

Stele: Bundles collateral; clusters of bast lie within the older, and around the young, phloem; these tissues are enclosed by wood rays which pass as radii from the center of the root toward the bark, joining in arches around phloem; xylem with irregular clusters of large tracheae; few small wood parenchyma cells; compact, small wood fibers prominent.

Summary: Cork prominent; parenchyma little; mechanical tissue in form of bast and wood fibers, forming a tough, compact root.

Baptisia leucantha T. and G.

Habitat: Alluvial basin; moist, subject to drought; perennial.

Gross structure: Long, thick tap root with horizontal surface, fleshy branches; tough; tubercled; perennial.

Histology of root (Plate XXIII, fig. 1):

Primary cortex: Depth 1/2 radius of root; thin band hypodermal cork; large oval-celled starch parenchyma with scattered clusters of bast cells; endodermis not distinct.

Stele: Radial bundles; several concentric zones of bast cells laid down in clusters bordering the new phloem and lying within and around the older phloem; broad rows of wood rays of long parenchyma cells extending radially into cortex,

spreading in fan-shaped areas of parenchyma; tracheae large, prominent; wood fibers conspicuous among wood parenchyma.

Summary: Cortex thick; mechanical tissue prominent; tracheae large, numerous; compact.

Desmodium illinoense Gray.

Habitat: Slopes; moist to dry.

Gross structure: Thick tap fibrous root; branched, tough; tubercled; perennial.

Histology of root:

Primary cortex: Depth 1/6 radius of root; narrow band of hypodermal cork; parenchyma thin-walled.

Stele: Radial bundle; wide rows of long, rectangular cells form wood rays which extend through xylem radially to bark where they form arches around phloem; annual rings prominent; wood parenchyma little; wood fibers abundant; tracheae large but few; large protoxylem and smaller metaxylem tissues of the primary xylem show the exarch character of the bundle.

Summary: Small cortex; prominent stele with much mechanical tissue in form of wood fibers; wood rays prominent; tracheae not conspicuous; compact.

Violaceae

Viola pedata L.

Habitat: Hill crests and slopes; dry, gravelly soil.

Gross structure: Rootstock short; erect; not scaly.

Histology of rhizome (Plate XXV, fig. 1):

Primary cortex: Depth 1/4 radius of root; hypodermal cork 2 or 3 rows; parenchyma large-celled, thin-walled; endodermis not distinct.

Stele: Vascular bundles distinct; collateral; separated by parenchyma rays which extend into the large pith cylinder; tracheae numerous, small; wood parenchyma thin-walled; pith parenchyma large-celled, round to oval; fairly compact.

Summary: Parenchyma prominent; mechanical tissue absent; tracheae small, numerous.

Gentianaceae

Gentiana puberula Michx.

Habitat: Moist slopes, upland mostly.

Gross structure: Slender rhizome bearing fascicles of relatively thickened roots.

Histology of root (Plate XXIII, fig. 2):

Primary cortex: Depth 1/2 radius of root; epidermal cells small, rectangular, thin-walled; 2–3 rows hypodermal collenchyma; large roundish parenchyma cells, fairly compact; endodermis not distinct.

Stele: Radial bundles, scattered clusters of phloem surrounded by large parenchyma cells; vascular cylinder small; tracheids numerous; remains of primary xylem show exarch character of primary bundle.

Summary: Parenchyma prominent, tracheae few; mechanical tissue absent.

Asclepiadaceae

Asclepias verticillata L.

Habitat: Alluvial basin; low prairie, moist soil.

Gross structure: Slender, radially extensive rhizome, bearing fascicles of thickened roots.

Histology of rhizome (Plate XXII, fig. 3):

Primary cortex: Depth 1/4 radius of rhizome; thick-walled, oval-celled parenchyma; endodermis not distinct.

Stele: Collateral bundles; phloem zone thin, unprotected, cells more or less crushed; xylem with few large tracheae; compact network of wood parenchyma;

small area of large-celled pith parenchyma into which project the remnants of the endarch xylem.

Summary: Parenchyma prominent; cortex relatively thick; mechanical tissue absent; tracheae few.

Labiatae

Monarda fistulosa L.

Habitat: Moist to dry slopes.

Gross structure: Elongated, slender, radially extensive rhizome, cross section square.

Histology of rhizome (Plate XXIV, fig. 1):

Primary cortex: Depth 1/4 radius of cylinder; epidermis of rectangular cells with uniformly thickened walls; hypodermal clusters of collenchyma cells in corners of square stem; parenchyma cells round, thin-walled; endodermis thin-walled.

Stele: Collateral bundles; vascular band very thin; 6-sided phloem cells protected by collenchyma; tracheae few; wood parenchyma small-celled; band of collenchyma separates xylem from pith; pith parenchyma of large, round, thin-walled cells.

Summary: Parenchyma prominent; mechanical tissue sparse; tracheae few.

Compositae

Vernonia fasciculata Michx.

Habitat: Alluvial basin; low wet ground.

Gross structure: Radially elongated, extensive rhizome with clusters of thick fascicled roots.

Histology of rhizome (Plate XXVII, fig. 1):

Primary cortex: Depth 1/2 radius of vascular cylinder; collateral bundles; epidermis of rectangular, uniformly thickened cells; hypodermis, 2–3 rows collenchyma; aerenchyma with branched sclerids at intervals; endodermis thin-walled.

Stele: Collateral bundles; phloem capped with clusters of bast; xylem fascicles separated by thick strands of rectangular-celled wood rays; tracheae few; wood parenchyma thick-walled, compact; wood fibers present; primary endarch bundle distinct; pith aerenchyma with scattered sclerids.

Summary: Aerenchyma prominent; tracheae inconspicuous; mechanical tissue fairly well developed.

Histology of root (Plate XXVII, fig. 2):

Primary cortex: Depth 5/6 of root; epidermis uniformly thickened; aerenchyma fills most of cortical space; endodermis thin-walled.

Stele: Radial bundles; small area of pith in center; tracheae few.

Summary: Aerenchyma prominent; cortex deep; vascular tissue limited.

Aster azureus Lindl.

Habitat: Hill crests and slopes.

Gross structure: Abbreviated rhizome, hard; clusters of roots form a thick fringe along the sides.

Histology of rhizome (Plate XXVI, fig. 2):

Primary cortex: Depth 1/7 radius of root; epidermis with horny, cuticularized edge; 3–4 rows hypodermal cork; zone of elongated collenchyma cells.

Stele: Bundles radial; thin-walled parenchyma bearing glands surrounds the phloem ring; bundles tipped with bast; xylem strands appear branched; traversed by annular rings of thin parenchyma; wood fibers strengthen xylem; broad wood rays of elongated parenchyma cells prominent; pith of large, rather thick-walled cells; primary endarch xylem distinct.

Summary: Mechanical tissue fairly prominent; xylem compact.

Artemisia ludoviciana (Nutt.) Riddell.

Habitat: Hillsides.

Gross structure: Slender, hard rhizome with clusters of filamentous roots.

Histology of rhizome (Plate XXIV, fig. 2):

Primary cortex: Depth 1/4 radius of root; cork 4 rows; parenchyma compact.

Stele: Bundles radial, distinct; phloem protected by patches of bast; vessels few; wood parenchyma cells large; bast sheath prominent; pith parenchyma compact.

Summary: Parenchyma well developed but compact; mechanical tissue conspicuous around bundle; xylem tissue sparse.

Antennaria plantaginifolia (L.) Richards.

Habitat: Dry hill crests and slopes.

Gross structure: Slender, radially extensive rhizomes with fringes of slender roots at their nodes.

Histology of rhizome (Plate XXVI, fig. 1):

Primary cortex: Depth 1/4 of radius of root; cork 1/4 of cortex; parenchyma thin-walled, rectangular; endodermis thin-walled.

Stele: Collateral bundles; phloem unprotected, rectangular cells; thick parenchyma rays separate the bundles; xylem with annular rings marked by layers of wood parenchyma at beginning of ring and thick-walled wood fibers at end; pith parenchyma large-celled, rather spongy.

Summary: Cork well developed; mechanical tissue in form of wood fibers prominent.

Liatris squarrosa Willd.

Habitat: Slopes, rather dry.

Gross structure: Stem corm-like, hard, flinty; somewhat scaly on surface; bears clusters of small filamentous roots.

Histology of corm (Plate XXVIII, fig. 2):

Primary cortex: Depth 1/6 radius of corm; cork 1/7 of cortex; cortical parenchyma of brick-like cells among which are a few sclerids; resin ducts present, bordered by 2 rows of thin parenchyma cells; endodermis not distinct.

Stele: Collateral bundles; clusters of sclerenchyma cells arranged around the perimeter of the phloem strands; parenchyma thin-walled; xylem in a series of clusters of annular growth; clusters of wood parenchyma and tracheae formed in spring; wood fibers formed in fall; xylem surrounded by fairly thick-walled, elongated parenchyma cells; resin ducts numerous throughout parenchyma; central pith of roundish cells.

Summary: Mechanical tissue prominent; resin ducts conspicuous; parenchyma compact.

Solidago canadensis L.

Habitat: Moist slopes; sometimes dry places.

Gross structure: Abbreviated rhizome with slender clusters of short roots.

Histology of rhizome:

Primary cortex: Depth 1/6 radius of rhizome; hypodermis of mechanical cells; parenchyma rather thick-walled; endodermis not distinct.

Stele: Collateral bundles; points of bast above tips of phloem; xylem fascicles branched outside of the second annular ring; broad bands of wood parenchyma cells separate the bundles; zones of parenchyma cells are left in spring growth; wood fibers appear in bands in fall growth.

Summary: Mechanical tissue prominent; tracheae fairly large.

Histology of root:

Primary cortex: Depth 1/2 radius of root; thick band collenchyma; parenchyma fairly thick-walled; endodermal walls not thickened.

Stele: Radial bundles show exarch arrangement of primary xylem; mechanical tissue fills center of cylinder; tracheae large.

Summary: Cortex deep; conspicuous mechanical tissue; large tracheae.

Heliopsis scabra Dunal.

Habitat: Dry to moist slopes.
Gross structure: Tuber-like rhizome; rather short; radial extension; bears clusters of small roots.
Histology of rhizome (Plate XXV, fig. 2):
Primary cortex: Depth 1/9 radius rhizome; hypodermal collenchyma; scattered sclerenchyma among the elongated parenchyma; endodermis walls of uniform thickness.
Stele: Collateral bundles; xylem fascicles branched above the first annual ring; broad rows of rectangular-formed wood rays separating the bundles or branches thereof; tracheae numerous; wood fibers prominent; primary endarch xylem distinct; pith parenchyma cells hexangular.
Summary: Mechanical tissue prominent; structure of stem compact.

Lepachys pinnata (Vent.) T. & G.
Habitat: Slopes; moist to dry.
Gross structure: Abbreviated rhizome; hard; clusters of slender roots.
Histology of rhizome (Plate XXVIII, fig. 1):
Primary cortex: Depth 1/6 radius of rhizome; parenchyma with clusters of sclerenchyma; endodermis not distinct.
Stele: Collateral bundles; xylem fascicles branched; separated radially and sometimes transversely by wood rays of parenchyma; tracheae few, small; wood parenchyma prominent; pith parenchyma with clusters of sclerids scattered through it.
Summary: Mechanical tissue abundant; tracheae small, few; parenchyma rays conspicuous.
Histology of root:
Primary cortex: Depth 1/2 radius root; parenchyma with sclerenchyma cells scattered through; endodermis not distinct.
Stele: Tracheae prominent; wood fibers abundant.
Summary: Mechanical tissue prominent; cortex deep.

Helianthus tuberosus L.
Habitat: Moist slopes.
Gross structure: Slender, radially extensive rhizomes; tuberous.
Histology of rhizome (Plate XXVII, fig. 3):
Primary cortex: Depth 1/4 radius of root; hypodermis of collenchyma; parenchyma large-celled, loose; resin glands scattered through parenchyma; endodermis not distinct.
Stele: Collateral bundles; phloem tipped with patches of sclerenchyma; tracheae few; woody parenchyma sparse, rather thick-walled; pith parenchyma of large, round cells, loose; resin glands scattered among pith.
Summary: Parenchyma prominent; mechanical tissue sparse.

Analysis of the Anatomy of Subterranean Organs

Of the twenty-six subterranean organs studied, fifteen were upland plants and eleven were plants of the alluvial basin.

Alluvial basin species: *Typha latifolia, Phragmites communis, Spartina Michauxii, Panicum virgatum, Scirpus fluviatilis, S. validus, Iris versicolor, Polygonum Muhlenbergii, Ranunculus delphinifolius, Vernonia fasciculata, Asclepias verticillata.*

Upland species: *Heuchera americana, Potentilla arguta, Petalostemum candidum, Baptisia leucantha, Desmodium illinoense, Gentiana puberula,*

Asclepias verticillata, Monarda fistulosa, Aster azureus, Liatris squarrosa, Solidago canadensis, Heliopsis scabra, Helianthus tuberosus, Monarda fistulosa, Artemisia ludoviciana.

The terminal or absorbing roots of four plants were studied and others were examined. The structure of the four roots drawn is typical and may be summarized as having a deep cortex (in this case 4/5–5/6 the radial depth of the stem) of aerenchyma or loose parenchyma, only a trace of, or no, mechanical tissue, and a variable vascular tissue with reference to the size and number of tracheae. It is evident that the function of these roots is absorption only. There is usually a little mechanical tissue in the upland species and a little more specialization of the vascular tissue.

Ranunculus multifidus has entirely a fibrous root and retains the primitive root character to maturity. It has no mechanical tissue.

Of the root structures studied, six were of upland plants and one of an alluvial basin plant. (Most of the prominent alluvial basin plants have rootstocks). Here parenchyma, found only in the cortex, was compact, reduction in space being supplemented by the presence of cork, collenchyma, or mechanical tissue. Reduction or absence of mechanical tissue was

Comparison of Tissues of the Subterranean Organs

Roots

Name	Habitat	Root	Radial Depth Cortex	Parenchyma	Mechanical Tissue	Vascular Tissue
Typha latifolia	Al. bas.	Terminal	4/5	Aerenchyma	None	Fairly prominent
Phragmites communis	Al. bas.	Terminal	5/7	Aerenchyma	Trace	Distinct; not prominent
Iris versicolor	Al. bas.	Terminal	5/6	Aerenchyma	Moderate	Fairly prominent
Vernonia fasciculata	Al. bas.	Primary	1/2	Aerenchyma prominent; parenchyma	Moderate	Limited; tracheae few
Ranunculus delphinifolius	Al. bas.	Main fibrous	4/5	Aerenchyma	None	Limited
Polygonum muhlenbergii	Al. bas.	Primary	1/4	Spongy cork	Moderate	Tracheae numerous
Lepachys pinnata	Upland	Terminal	1/2	Fairly compact	Slight	Tracheae prominent
Potentilla arguta	Upland	Primary	1/6	Compact	Prominent	Tracheae large, numerous
Desmodium illinoense	Upland	Primary	1/6	Slight cork	Prominent in stele	Tracheae large, few
Petalostemum candidum	Upland	Primary	1/6	Thick-walled cork	Prominent	Tracheae large, numerous
Gentiana puberula	Upland	Primary	1/2	Prominent	Absent	Tracheae few
Solidago canadensis	Upland	Secondary	1/2	Parenchyma thick-walled	Prominent	Tracheae large
Baptisia leucantha	Al. bas.	Primary	1/2	Prominent	Moderate	Tracheae few

Subterranean Stems

Name	Habitat	Subterranean Stem	Radial Depth Cortex	Parenchyma	Mechanical Tissue	Vascular Tissue
Typha latifolia	Al. bas.	Rhizome	1/2	Aerenchyma	Slight in vas. bund. sheath	Fairly prominent
Phragmites communis	Al. bas.	Rhizome	1/2	Aerenchyma	Slight	Few bundles
Spartina Michauxiana	Al. bas.	Rhizome	3/7	Slight	Prominent	Vas. bundles large, numerous tracheae
Panicum virgatum	Al. bas.	Rhizome	2/9	Slight	Prominent	Vas. bundles large
Scirpus fluviatilis	Al. bas.	Rhizome	1/2	Aerenchyma	In vas.bund. sheaths	Vas. bundles numerous
Scirpus validus	Al. bas.	Rhizome	1/3	Aerenchyma	In vas.bund. sheaths	Prominent
Iris versicolor	Al. bas.	Rhizome	1/3	Aerenchyma	In vas.bund. sheaths	Prominent
Polygonum Muhlenbergii	Al. bas.	Rhizome	1/6	Aerenchyma	Absent except few wood cells	Slight
Asclepias verticillata	Al. bas.	Rhizome	1/4	Prominent	Absent	Tracheae few
Monarda fistulosa	Al. bas.	Rhizome	1/4	Prominent	Slight	Tracheae few
Heuchera Americana	Upland	Rhizome	1/5	Prominent	Absent	Tracheae; tissue small
Viola pedata	Upland	Rhizome	1/4	Prominent	Absent	Tracheae small, numerous
Aster azureus	Upland	Rhizome	1/7	Cork slight; parenchyma	Fairly prominent	Tracheae numerous
Antennaria plantaginifolia	Upland	Rhizome	1/4	Moderate	Prominent wood fibers	Tracheae small, inconspicuous
Liatris squarrosa	Upland	Corm	1/6	Compact	Prominent	Few tracheae; small
Heliopsis scabra	Upland	Rhizome	1/9	Slight	Prominent	Tracheae numerous
Lepachys pinnata	Upland	Rhizome	1/6	Slight	Prominent	Tracheae small, few
Artemisia ludoviciana	Upland	Rhizome	1/4	Prominent	Moderate	Few tracheae
Helianthus tuberosus	Upland	Rhizome	1/4	Prominent	Slight	Tracheae few

prominent in 66 percent of the roots. Tracheae were generally large and quite numerous.

The only thick root of the alluvial basin studied was that of *Baptisia leucantha*, which had prominent parenchyma, moderate mechanical tissue, and few tracheae.

The subterranean stems of ten alluvial basin and nine upland plants were examined. Of the alluvial basin plants, 65 percent had aerenchyma and only 10 percent reduced parenchyma. In only 10 percent was mechanical tissue prominent though present about the sheaths of monocotyledons. In the monocotyledons the vascular tissue was fairly prominent; in dicotyledons it was poorly developed.

In the stems of the upland plants there is considerable variation in the

relative proportion of parenchyma, though in the plants of the drier habitats it was present in very slight degree. Mechanical tissue was prominent in most of the plants with large aerial portions, and usually absent in the low-growing plants with the exception of Helianthus which seems to be a non-conformist in both leaf and stem characters and lives by a code of its own. The tracheae were also variable in size and number. In this small group of plants no correlation could be seen between the number of tracheae and the number of leaves. The presence of thick-walled cells not only serves as a reinforcing character but no doubt tends to preserve turgor and to protect water-conducting tissues against loss of water.

SUMMARY

A study of the minute anatomy of subterranean organs of prairie plants shows:

(1) There is a tendency to the production of prominent mechanical tissue in plants of dry habitats and reduction of parenchymatous tissue.

(2) In moist habitats the proportion of parenchymatous tissue is prominent. Aerenchyma is abundant in swamp plants.

(3) The vascular tissue is variable in quantity, seemingly more or less subject to systematic variation.

The subterranean stem is predominant as an equivalent of the primary root, especially in moist lowland regions. It is more efficient than the root in propagation. Primary roots which show secondary thickening resemble stems in their concentric manner of expansion. The stem has an area of pith which serves as a reservoir for water and hence increases its efficiency for radial distribution.

I wish to acknowledge the helpful comment of Dr. L. H. Pammel, Dr. J. N. Martin, and Miss Charlotte M. King in the preparation of this paper.

IOWA STATE COLLEGE,
AMES, IOWA

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EXPLANATION OF PLATES XV–XXVIII

A, aerenchyma; *B*, bast; *C*, collenchyma; *CM*, cambium; *CK*, cork; *EN*, endodermis; *EP*, epidermis; *P*, parenchyma; *PH*, phloem; *RC*, resin canal; *SC*, sclerenchyma; *RH*, root hair; *T*, tracheae; *X*, xylem; *PX*, protoxylem; *MX*, metaxylem; *WF*, wood fibers; *WP*, wood parenchyma; *WR*, wood rays; *VB*, vascular bundle.

The figures were made with the aid of a camera lucida. The compound microscope was a Spencer, Oculars 5× and 10× and objectives 4 and 16, with a standard tube length, were used in various combinations.

PLATE XV

Subterranean Systems of Water Plants

FIG. *a*. *Polygonum Muhlenbergii.*
FIG. *b*. *Phragmites communis.*
FIG. *c*. *Scirpus fluviatilis.*
FIG. *d*. *Typha latifolia.*
FIG. *e*. *Iris versicolor.*
FIG. *f*. *Sagittaria latifolia.*
FIG. *g*. *Scirpus validus.*
FIG. *h*. *Spartina Michauxiana.*

PLATE XVI

FIG. 1. *Typha latifolia*, rhizome, × 75.
FIG. 2. *Typha latifolia*, root, × 93.

PLATE XVII

FIG. 1. *Phragmites communis*, rhizome, × 150.
FIG. 2. *Phragmites communis*, root, × 115.

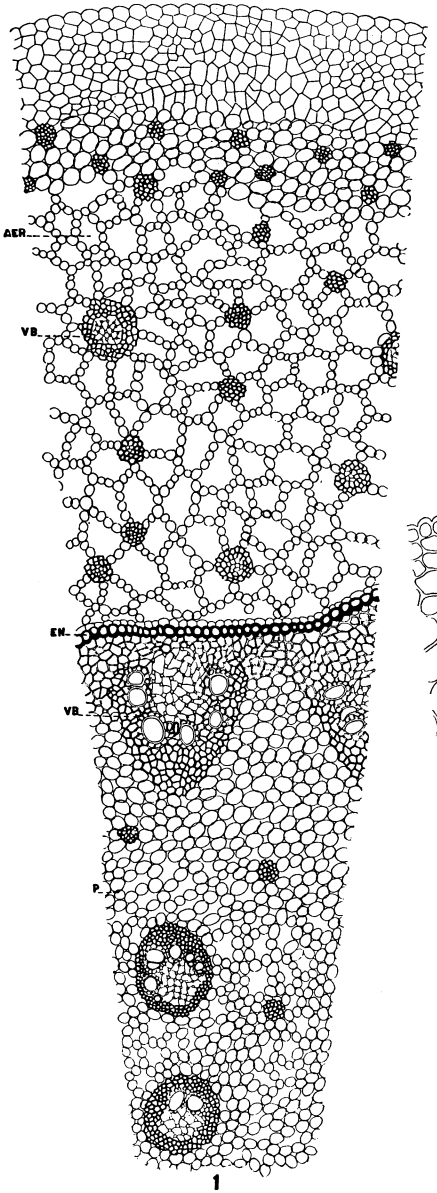
PLATE XVIII

FIG. 1. *Spartina Michauxiana*, rhizome, × 125.
FIG. 2. *Panicum virgatum*, rhizome, × 102.

PLATE XIX

FIG. 1. *Iris versicolor*, rhizome, × 50.
FIG. 2. *Iris versicolor*, root, × 75.
FIG. 3. *Scirpus fluviatilis*, rhizome, × 50.

HAYDEN: ECOLOGIC ANATOMY.



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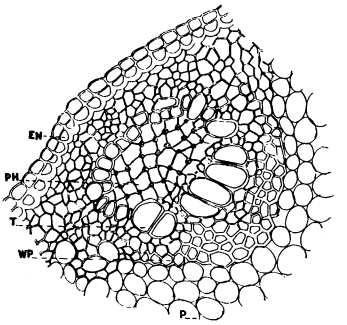

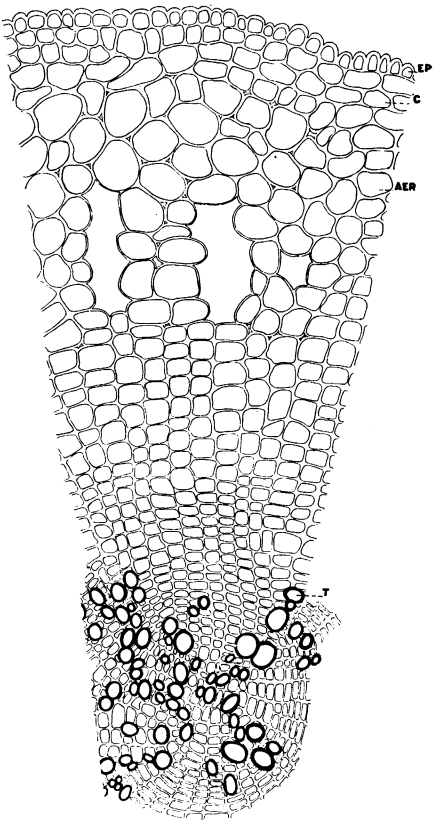

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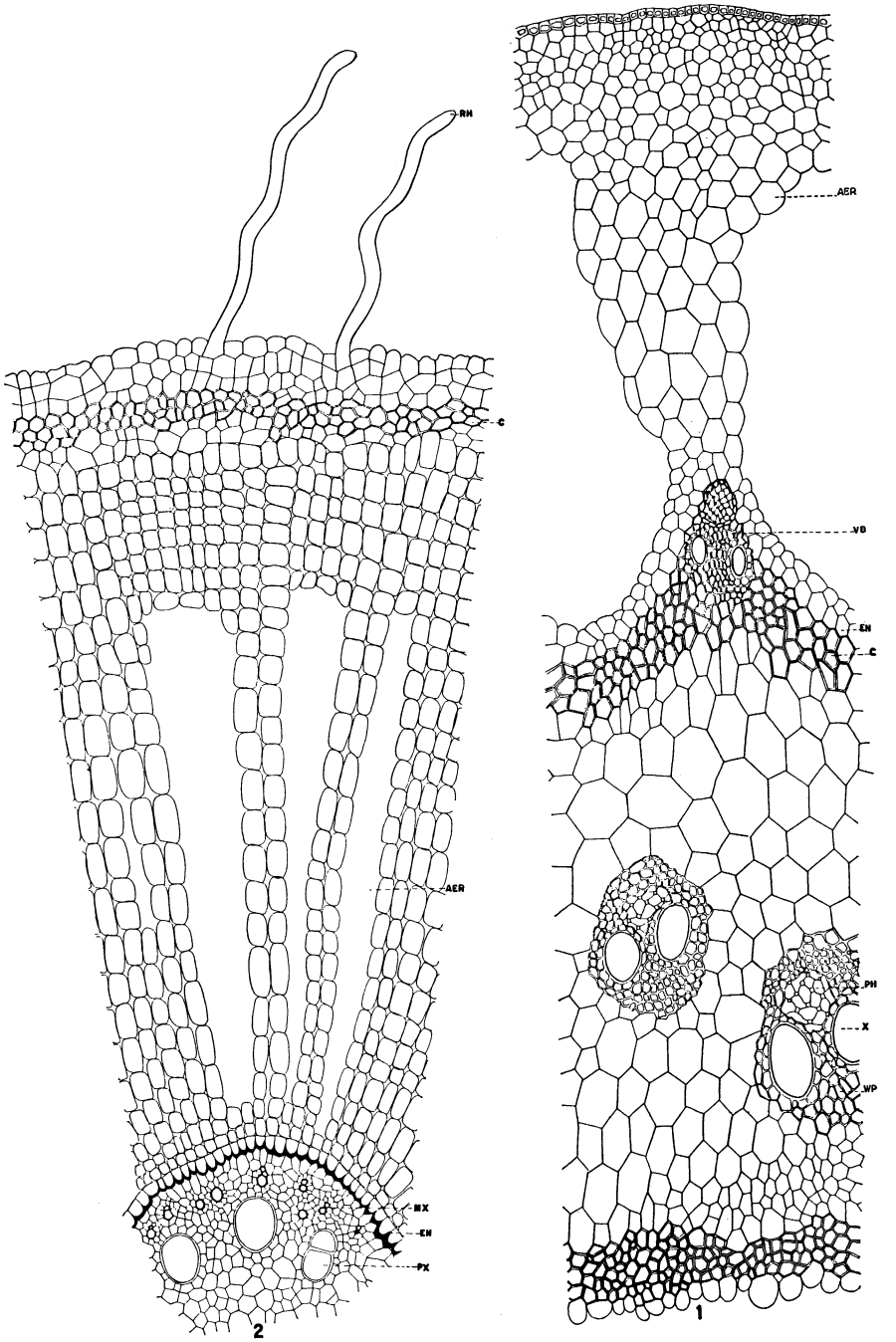

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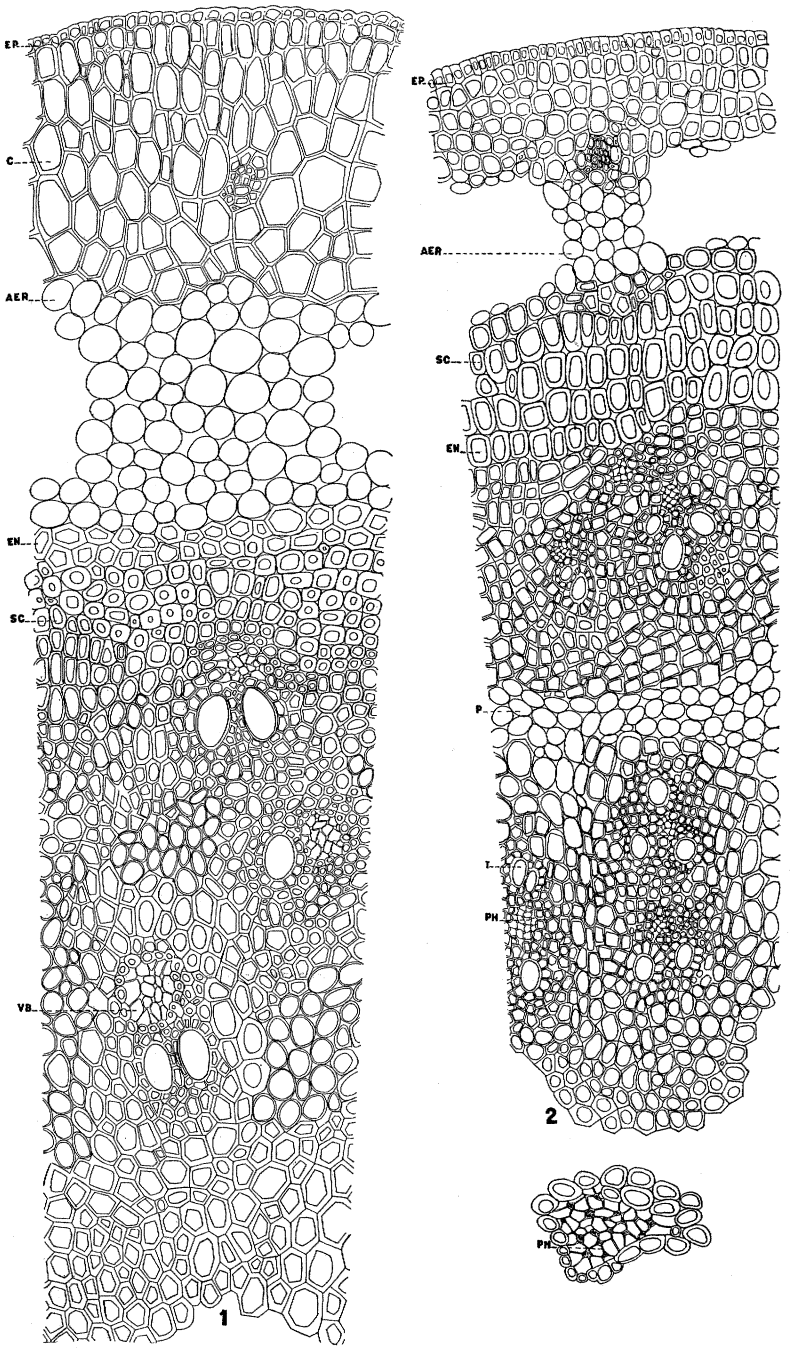

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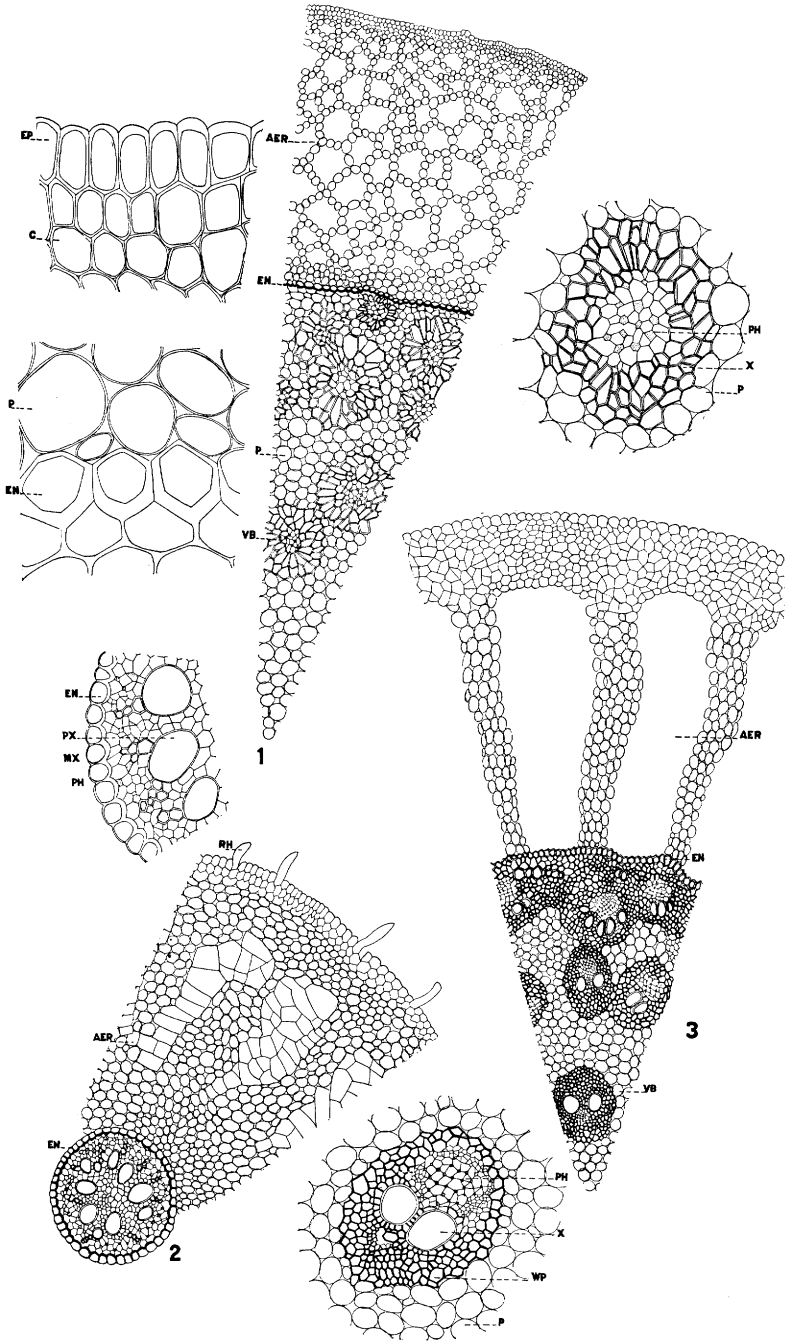

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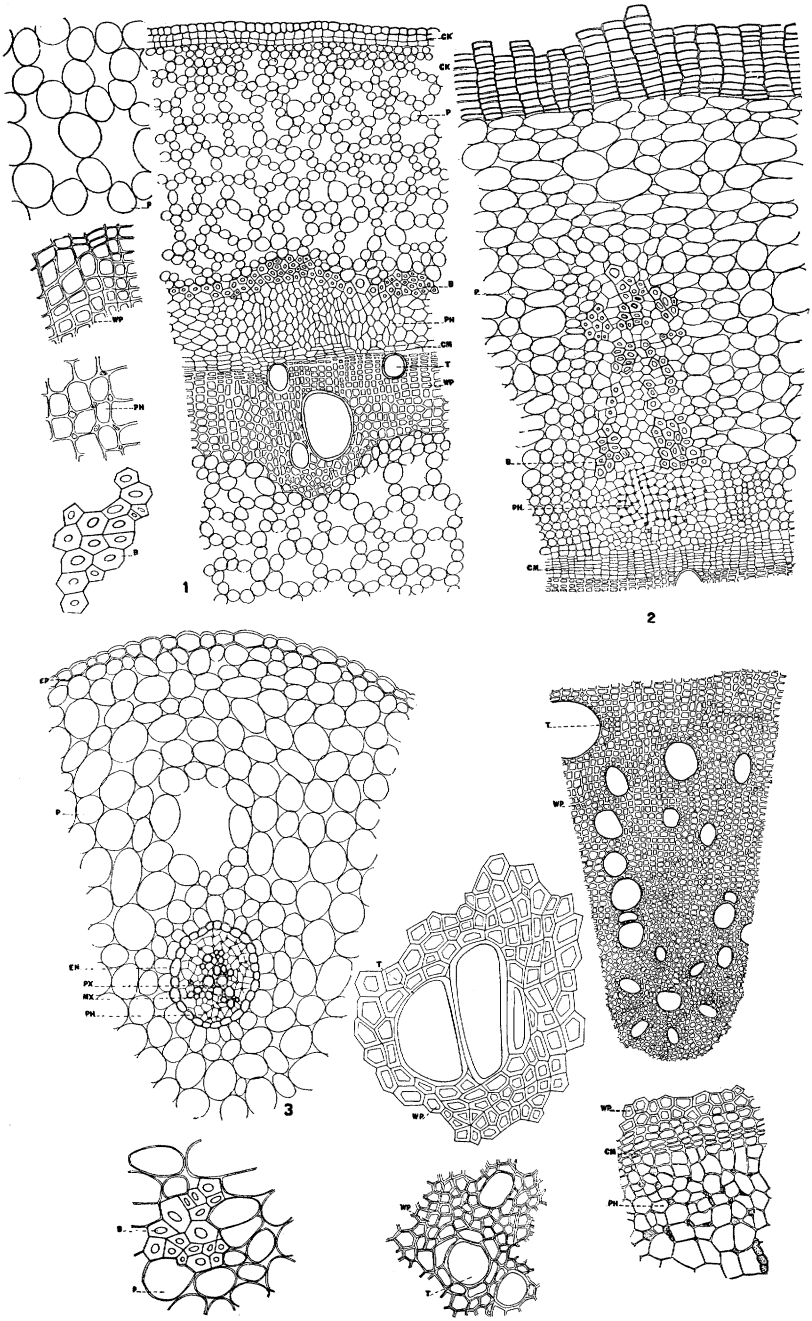

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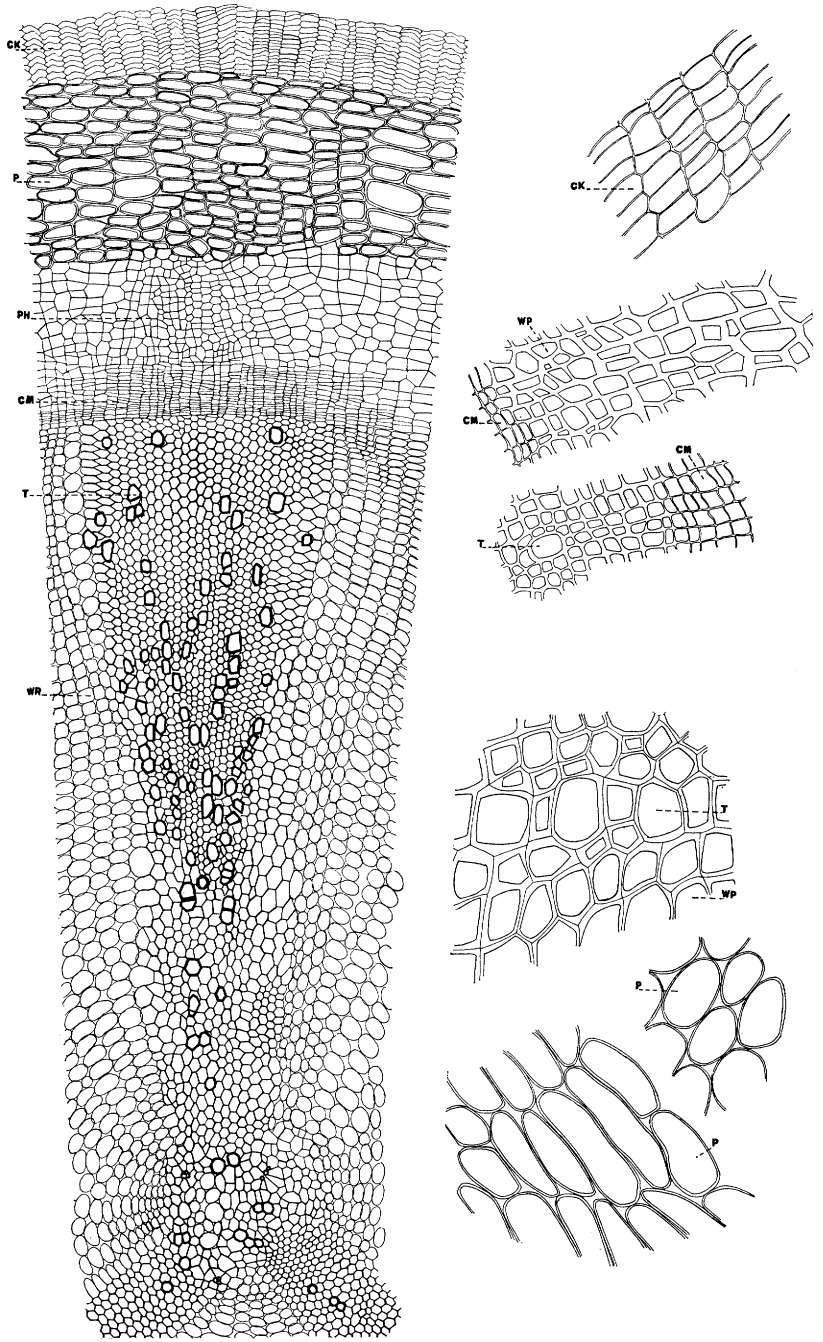

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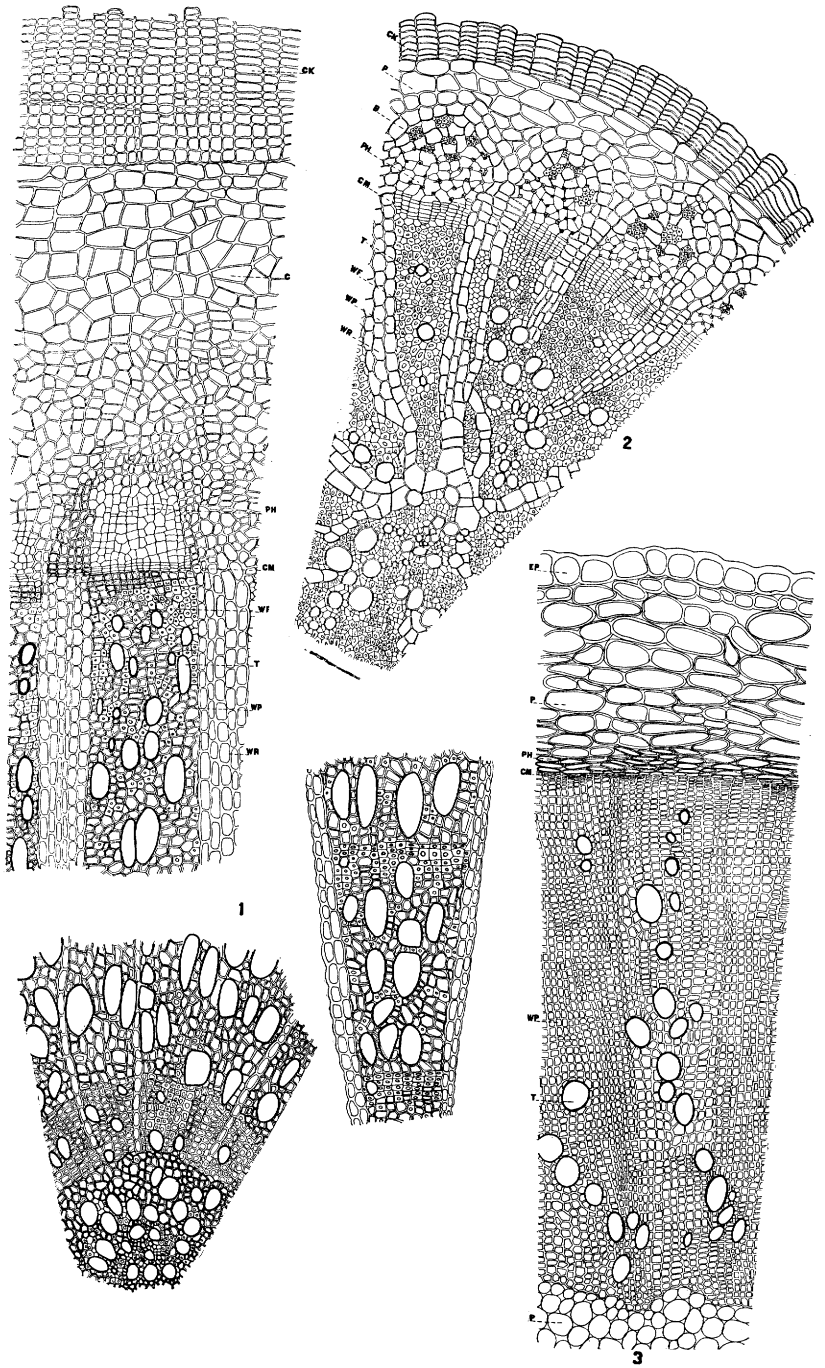

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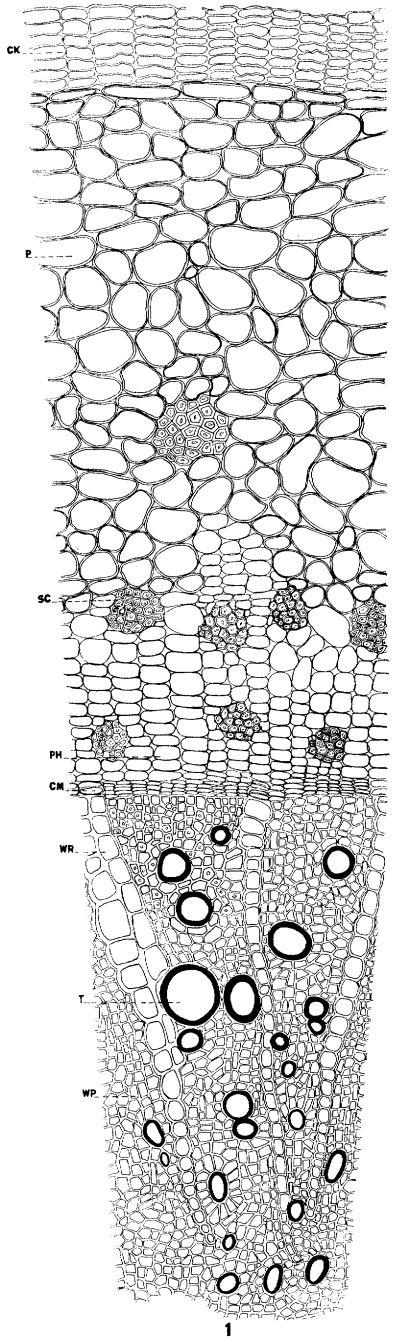

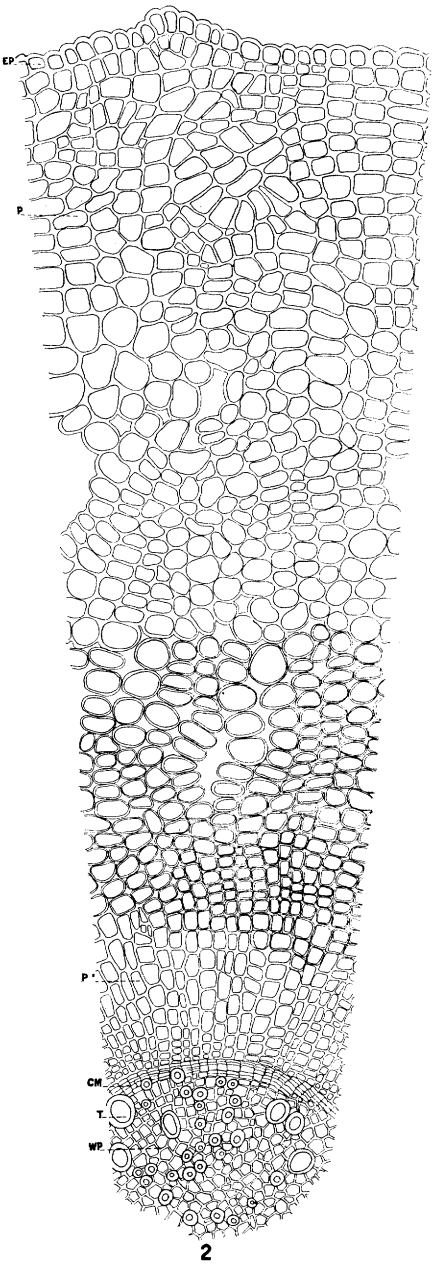

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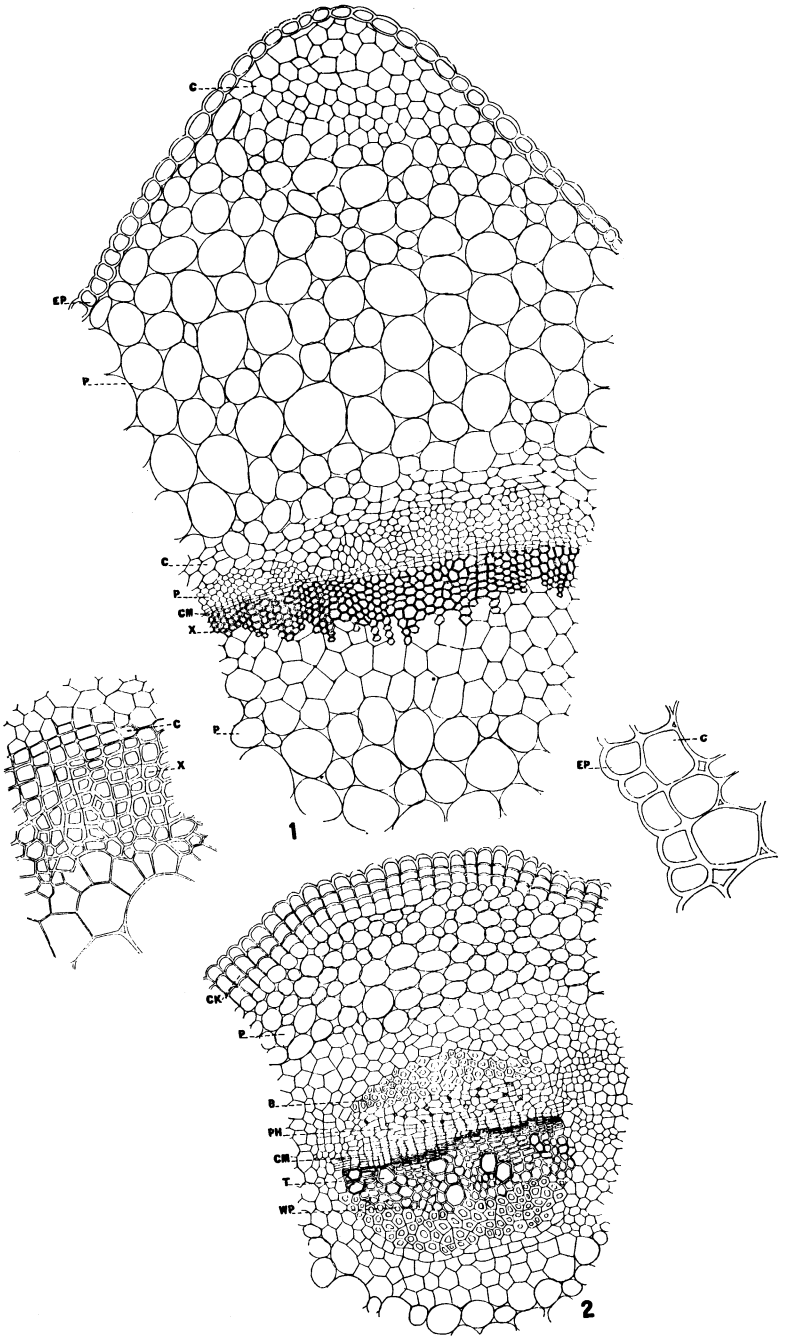

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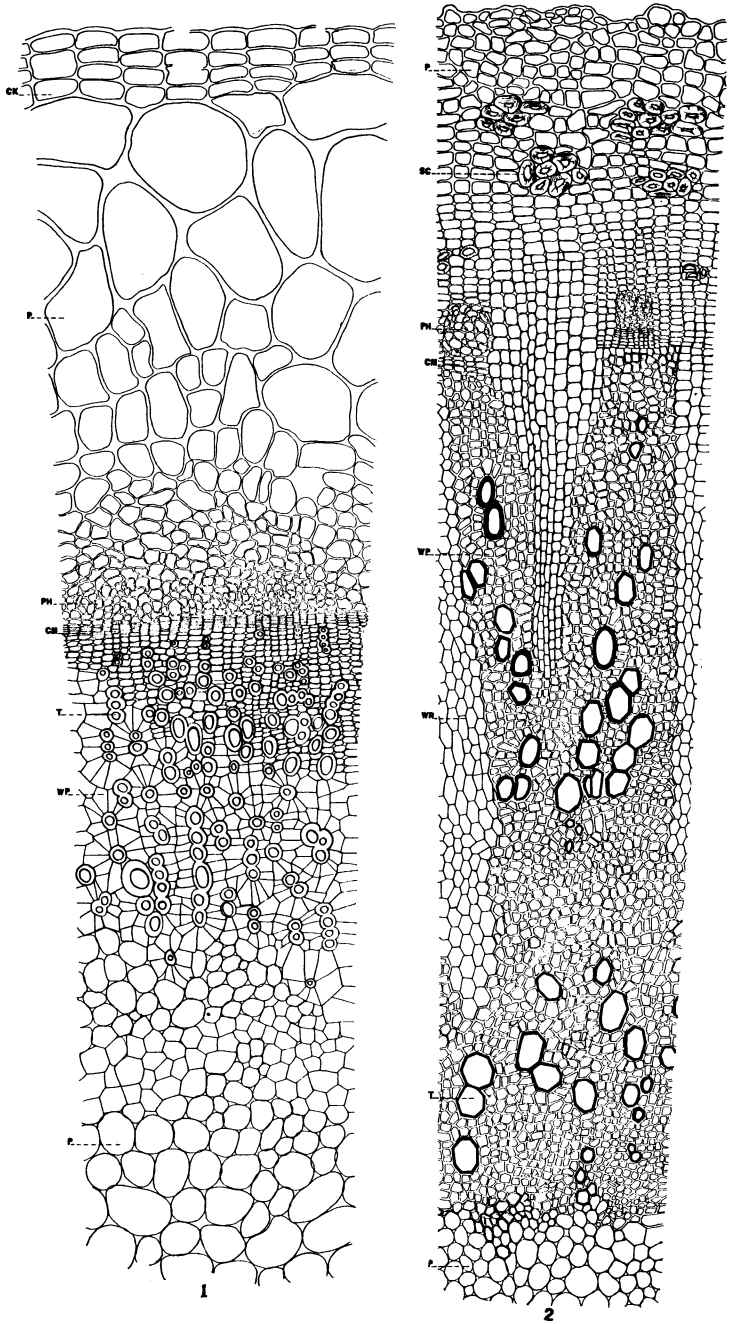

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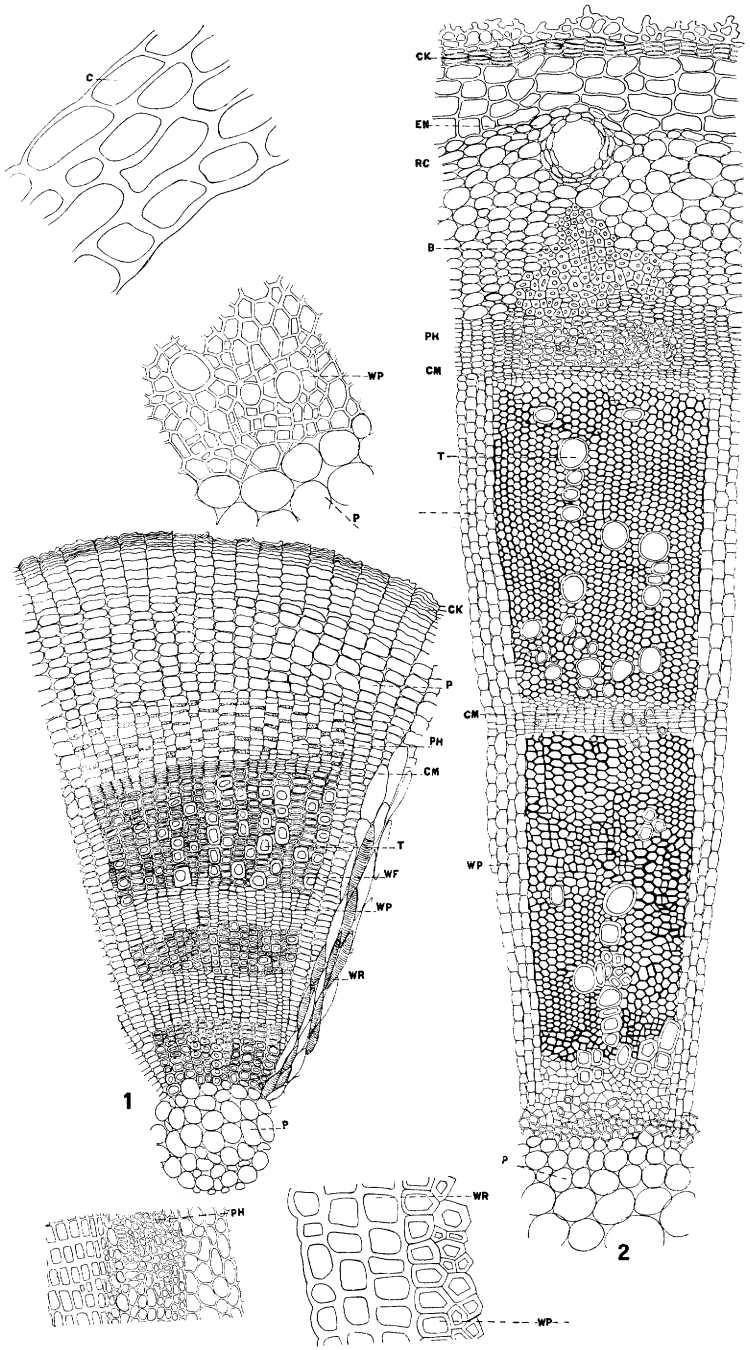

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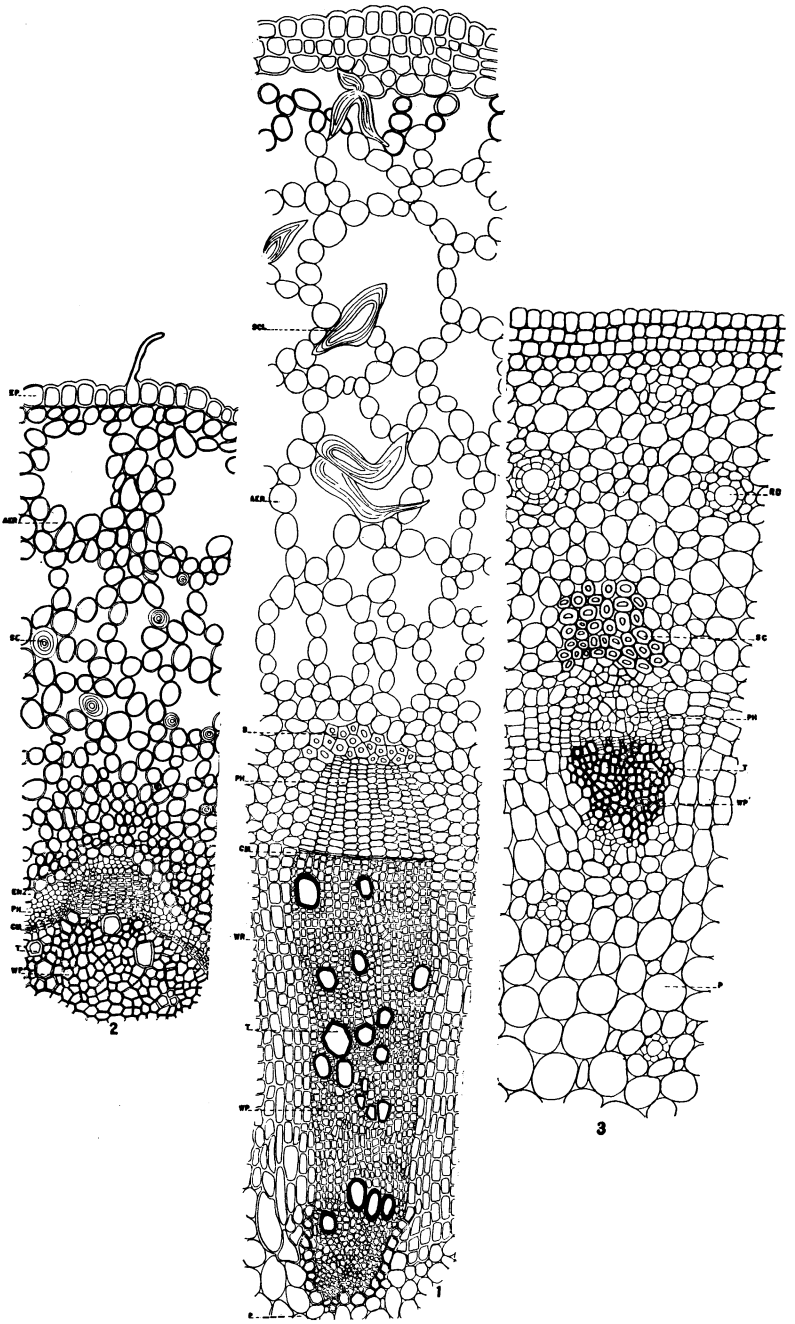

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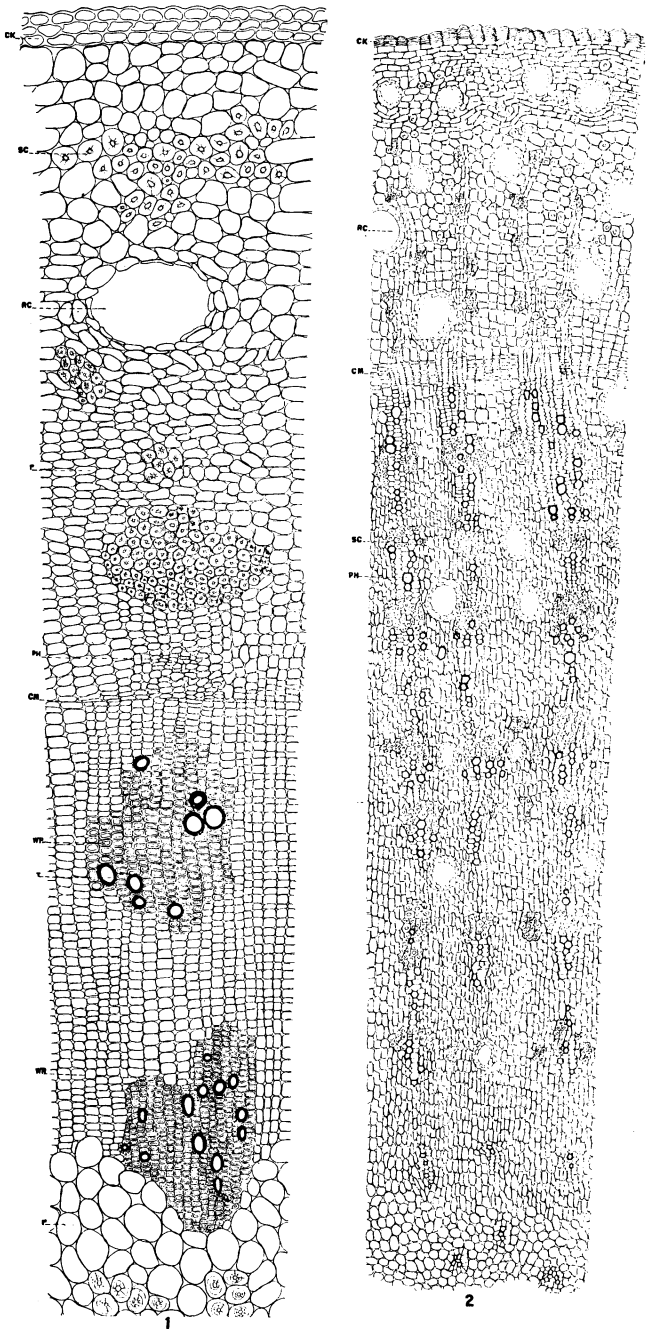

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PLATE XX

FIG. 1. *Polygonum Muhlenbergii*, rhizome, × 45.
FIG. 2. *Polygonum Muhlenbergii*, root, × 45.
FIG. 3. *Ranunculus delphinifolius*, root, × 100.

PLATE XXI

FIG. 1. *Heuchera americana*, rhizome, × 80.

PLATE XXII

FIG. 1. *Potentilla arguta*, root, × 100.
FIG. 2. *Petalostemum candidum*, root, × 75.
FIG. 3. *Asclepias verticillata*, rhizome, × 75.

PLATE XXIII

FIG. 1. *Baptisia leucantha*, root, × 150.
FIG. 2. *Gentiana puberula*, root, × 150.

PLATE XXIV

FIG. 1. *Monarda fistulosa*, rhizome, × 125.
FIG. 2. *Artemisia ludoviciana*, rhizome, × 50.

PLATE XXV

FIG. 1. *Viola pedata*, rhizome, × 75.
FIG. 2. *Heliopsis scabra*, rhizome, × 90.

PLATE XXVI

FIG. 1. *Antennaria plantaginifolia*, rhizome, × 165.
FIG. 2. *Aster azureus*, rhizome, × 110.

PLATE XXVII

FIG. 1. *Vernonia fasciculata*, rhizome, × 60.
FIG. 2. *Vernonia fasciculata*, root, × 90.
FIG. 3. *Helianthus tuberosus*, rhizome, × 76.

PLATE XXVIII

FIG. 1. *Lepachys pinnata*, rhizome, × 85.
FIG. 2. *Liatris squarrosa*, corm, × 16.